Developmental Reaction Norms Predicted by Multiple Random Regression Model in a Sex-Separated Bivariate Analysis

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Introduction

Schlichting and Pigliucci (1998) defined the concept of developmental reaction norm (DRN) as the complete set of multivariate ontogenetic trajectories that can be produced by a single genotype exposed to all biologically relevant environments. The same authors considered the DRN as an ideal framework to understand the evolution of phenotypes through the elucidation of the developmental programs involved in the epigenetic transition from genotype to phenotype. The introduction of random regression models (RRM) in longitudinal data studies (Kirkpatric and Heckman (1989); Meyer (1998)) allowed predicting adaptive reaction norms by considering breeding values instead of phenotypic ones. Kirkpatrick and Meyer (2005) also considered multiple control variables to these models, so that a developmental dimension could be added in a single analysis. Besides, the evolutionary theory of sex proposed by Geodakyan (1974) foresees different reaction norms for males and females. This sexual dimorphism would depend on the environmental heterogeneity and the population dispersion. It can mislead the current selection applied to cattle breeding, where sex is considered as a fixed effect, because traditional evaluations are not able to identify environment-dependent sexually divergent breeding values. In this work, the Nelore cattle weight trait was assessed by using multiple random regression model in an adaptive developmental reaction norm (ADRN) approach, with separate male and female progeny records for a bivariate analysis.

Material and methods

Original dataset. The initial dataset had 1,110,662 weights from 408,416 animals collected from 1974 to 2006, in 366 Brazilian herds, by ANCP (Associação Nacional de Criadores e Pesquisadores) for the Brazilian Nelore Cattle Genetic Improvement Program (Nelore Brasil). The numerator relationship matrix was adapted to a sire model. Contemporary Groups (CGs) were defined by using information on sex, year, farm, management and calving season; CGs with less than six individuals were excluded.

Environmental descriptor. The environmental descriptor was calculated using the environmental group method presented by Pegolo et al. (2009): the farm-year-season-management group averages were standardized to a mean of zero and an standard deviation of one for each age; then, the standardized values were multiplied by ten and the

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environmental groups (EG) were obtained by considering only the integer part of those values. Records were separated according to sex. Univariate random regression analyses were proceeded with sex-separated adjusted weights for 120, 210, 365 and 450 days (W120, W210, W365 and W450), in order to apply the iterative algorithm proposed by Callus *et al.* (2004). Initially, the EG values below -15 were considered in EG = -15 (bottom limit) and those above +15, in EG = +15 (upper limit). For the subsequent analysis, the fixed effect (CG) solutions were used to position records on the respective EG. As the first iteration resulted in a wide data distribution along the environmental gradient, the EG limits were changed to -20 (bottom limit) and +20 (upper limit) from the second to the final iteration. The process was stopped when the correlation between the EG positions in the previous and current analyses was > 0.999.

Parameter estimation. Weight records from male progenies (MPA) and female ones (FPA) were maintained in separated datasets for bivariate analysis, but additional restrictions were added for parameter estimation. In each dataset, sires were excluded if (1) they had <70 progeny weights and (2) the progeny weight distribution along the environmental gradient was <20 EG units. After that, only 462,513 total progeny weights were considered. The covariance function (CF) coefficients were estimated by using a random regression model with multiple control variables (Meyer and Kirkpatrick (2005)). The model considered linear Legendre polynomials along an environmental gradient (EG), and quadratic ones along an age gradient (adjusted weights were positioned at 120, 210, 365 and 450 days after birth), with 20 residual classes, avoiding heteroscedasticity. BLUPF90 software (Mizstal (2003)) and its updates (GIBBS3F90) estimated the genetic parameters by Bayesian inference. The Monte Carlo Markov Chain was generated with 393,165 iterations, with a burn-in of 3,165 iterations. Means were calculated by variable effective chain sizes, based on independent chain size values.

Results and discussion

The genetic CF coefficient estimates (posterior distribution means) and correlations between them are shown in Table 1. The matrix coefficients correspond to intercept (I), environmental plasticity (EP: linear regression on EG), growth slope (GS: linear regression on age), and growth curvature (GC: quadratic regression on age). Female progeny analysis (FPA) had larger I and EP than male progeny analysis (MPA). Correlations among CF coefficients (within sex) indicated important connections among ADRN attributes, as between environmental plasticity (EP) and growth slope (GS) in MPA (r_g=0,49). Otherwise, FPA had lower correlation between the same coefficients (r_g=0,23). Correlations between the correspondent CF coefficients (across sexes, on the diagonal) had higher positive values for I, EP and GS and lower positive value for GC. This correlation matrix was not symmetric and revealed environment-dependent sexually divergent genetic variances. These results indicate divergent selection in unfavorable range of the environmental gradient at later ages. It can be understood in ANCP breeding program, since sires are selected by global breeding values in a higher intensity, and adult female selection is based on culling of dams, when they are non-adapted to the tropical pastures in the commercial herd conditions. Heritability estimates in the different analyses are shown in Figure 1. The MPA heritability surface showed lower levels (from 0.15 to 0.38), with a depression in unfavorable environments. In FPA, heritabilities were higher (from 0.17 to 0.59), with a very limited depression dislocated to unfavorable environments and to younger ages. These results are better explained by a larger residual variances (15 to 48% higher in MPA than in FPA) than by differences between punctual genetic variances. A better fit of female data to the linear random regression on the environmental gradient is observed and it confirmed the results from single control variable random regression models used in the reaction norm approach for different ages by Pegolo (2009).

Table 1: Estimates (posterior distribution means) of genetic CF coefficients (Intercept - I, Environmental Plasticity - EP, Growth Slope – GS, and Growth Curvature – GC) in Female Progeny Analysis (FPA) and Male Progeny Analysis (MPA), and correlations between them. Posterior distribution standard deviations are shown in parenthesis [α]

		FPA			
		I	EP	GS	GC
FPA	I	62.43 (7.15)	10.63 (2.42)	11.23 (1.80)	-3.22 (0.74)
	EP	0.46	8.65 (1.35)	1.25 (0.66)	-0.31 (0.33)
	GS	0.75	0.23	3.57 (0.56)	-0.31 (0.17)
	GC	-0.72	-0.18	-0.29	0.32 (0.09)
		MPA			
		I	EP	GS	GC
MPA	I	53.54 (6.29)	8.25 (2.27)	11.07 (1.80)	-2.51 (0.81)
	EP	0.39	8.08 (1.33)	2.90 (0.72)	-0.04 (0.35)
	GS	0.73	0.49	4.27 (0.67)	-0.08 (0.21)
	GC	-0.63	0.00	-0.07	0.3 (0.08)
		MPA			
		I	EP	GS	GC
FPA	I	0.77	0.23	0.54	-0.39
	EP	0.33	0.73	0.32	-0.13
	GS	0.23	0.21	0.85	-0.29
	GC	-0.19	-0.01	-0.15	0.26

[α] Genetic variance estimates on the diagonal, genetic covariance estimates and correlations above and below the diagonal, respectively, in first two matrices (within-sex). Only correlations are shown in the last matrix (across-sexes).

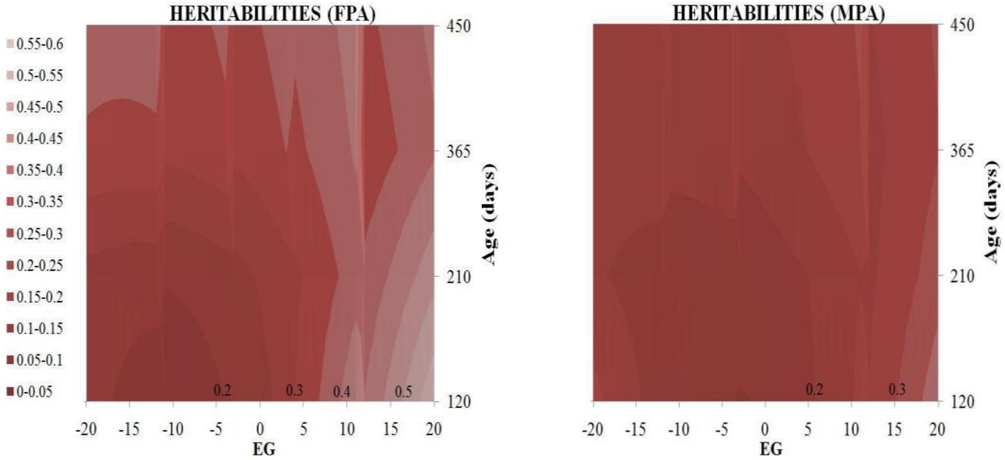

Figure 1: Heritability estimates along environmental groups (EG) at different days after birth (Age) in Female Progeny Analysis (FPA) and Male Progeny Analysis (MPA). Different levels are shown in a red scale according to the legend.

Conclusion

These results show important genotype by environment by sex by age interaction in weight trait for Nelore cattle in Brazilian herd environments. In these conditions, adaptive developmental reaction norms predicted by using female or male progeny records were different and indicated an environment-dependent sexually divergent selection. The multiple random regression model confirmed a higher heritability of environmental plasticity when it is analyzed by using female records in later ages.

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